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NOTES ON THE LIFE-HISTORY OF THE HACKBERRY BUTTERFLY, *ASTEROCAMPA CELTIS* (BDVL. & LEC.) ON SOUTH BASS ISLAND, LAKE ERIE (LEPIDOPTERA: NYMPHALIDAE)

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In 1950, when the Hackberry Butterfly became abundant on South Bass Island, it was identified for us by Dr. M. W. Boesel. We studied the life-history of this insect while it continued to be abundant, through 1954, recording accurately what we saw, and our records are presented as an addition to the facts previously known, most of which had been contributed by Riley (1874: 137), and Edwards (1884).

Edwards made his observations near Coalburgh, West Virginia, while Riley studied this butterfly in Missouri. Macy and Shepard (1941: 132) made records of this form in Minnesota, Clark and Clark (1951: 39) in Virginia, and Klots (1951: 120) farther south, without naming states. Our study was made at a point which is midway between Minnesota and Virginia, and nearly at the northern limits of distribution of the Hackberry Butterfly. Response to differences of climate at these parts of its range may explain variations in life history at the several sites where it has been studied. Unfortunately, Comstock's notes (1953: 127) on Arizona butterflies refer to different species, and cannot be applied to this one.

In the southern states, both the adults and the larvae hibernate, and the reproduction by these forms would yield young at two or three times during a summer. Holland (1904: 188) stated that this species is double-brooded in the more northern parts of the country, and that caterpillars produced from eggs laid by the second brood hibernate. This could have misled Macy and Shepard (1941) into thinking there were two generations, egg to egg, each year in Minnesota. Klots (1951) stated that there are three broods per year farther south. There has been but one generation per year, and but one brood on South Bass Island. No adults have hibernated, but the phenomenon of two "eat-outs" per year of hackberry tree leaves might have led to the other conclusion.

Edwards found larvae just out of hibernation, feeding upon a half-opened leaf bud of Hackberry on May 9, and butterflies from these larvae about the end of May. He also found a few faded and broken females very early in the season, and butterflies from eggs laid by these females by the middle of June. Riley found only larvae early in the season, in Missouri, and adults from these larvae by the middle of June. Eggs laid by these females hatched and the larvae thus produced fed for less than a month, then transformed and gave out a second brood of butterflies during August. Larvae from this second brood were the forms which hibernated. Riley's account is a clear record of two generations, though he calls them broods.

OBSERVATIONS

Most of the following observations were made in a woodlot near Lighthouse Point, on South Bass Island. Hackberry trees dominated the woodlot, and all but one of them were *Celtis occidentalis*, with its rough bark. There are many of these trees elsewhere on this island, but nowhere else does this species dominate an area as in this woodlot. Here the Hackberry Butterfly became so abundant, seasonally, that the odor of crushed leaves could be smelled by people on boats passing offshore, and, to anyone in the woods, the steady production of droppings sounded like rain.

There were year-to-year differences in behavior, and the data are tabulated to facilitate comparison, but the account is chronological, as recorded.



FIGURE 1. Hackberry branch, defoliated by butterfly larvae.



FIGURE 2. Hackberry Butterfly larvae descending tree trunk for pupation.

On June 14, 1950, the larvae had defoliated practically all of the hackberry trees in the woodlot, and on June 18, 1950, pupation was well under way. Butterflies emerged beginning June 25, and emergence reached its peak on June 28. Egg masses, some freshly-laid (yellow) and some ready to hatch (very dark) were found on the under surfaces of new, young hackberry leaves on July 13. First new larvae were found also on July 13, and by July 23 the young larvae were abundant on all trees in the woodlot. By August 20 the second "eat-out" had occurred, with nothing but veins left of the second foliation, and this condition persisted until the following spring (fig. 1).

No butterfly larvae could be found from the end of August, 1950, until June 10, 1951, but on that date there was considerable defoliation by larvae. On June 16, larvae, showing great differences in size, were actively migrating down the tree trunks (fig. 2) and up onto grasses, burdocks, basswoods, maples, and ash trees. They were pupating that day wherever they could attach to under surfaces, and, thereafter, few larvae were to be seen.

Pupa cases hung in great numbers throughout vegetation within 10 ft of the ground (fig. 3); one basswood leaf supported 40 of them. Many of the pupal cases persisted on the leaves throughout the season.

In 1951, the first butterfly appeared on June 23, and mating behavior was observed daily from June 28 through July 3. The following observations were made on June 28, at 2:00 PM, in bright sunlight. Males, distinguished readily from females by smaller size, darker color, more pointed wings and more slender abdomens, outnumbered females considerably. Females sought bright surfaces and there spread wide their wings, a position they maintained until they were being courted. Upon the approach of a courting male, a female raised the front of her body and lowered her abdomen until its tip touched the substrate. When a male approached such a female, he seemed to apply his mouthparts to the pos-



FIG. 3. Basswood branch bearing pupating larvae and pupae of the Hackberry Butterfly.

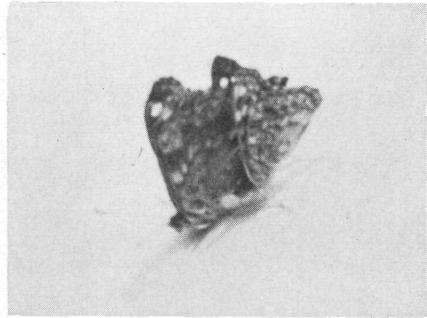


FIG. 4. Mating pair of Hackberry Butterflies.

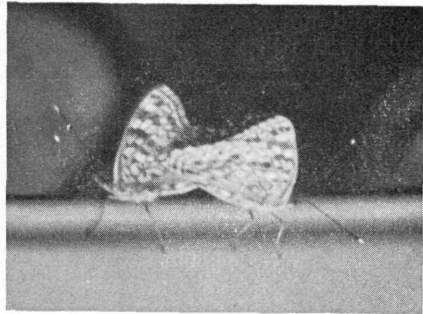


FIG. 5. Mated pair of Hackberry Butterflies.

terior edges of her wings, circling half-way around until his antennae touched hers; he then circled back behind her. As he approached her rear, she raised her wings to the vertical position. The male inserted his head between the upfolded wings of the female while trying to mate with her (fig. 4). They mated by his curving the posterior part of his body 180° so as to oppose his vent to hers, while the male's head was pointed in the same direction as that of the female. After mating was accomplished, he straightened his body so they faced in opposite directions, both with their wings folded, and they maintained this position for at least half an hour (fig. 5). When disturbed, the female flew away, carrying the male behind her. No observations were made on the interval between mating and egg-laying.

Two females were first found laying their piles of eggs at 1:00 PM, July 1. There were 310 and 356 eggs in each of two masses. One female laid all of her eggs in 37 minutes (1:35 to 2:12 PM).

New egg masses were seen on July 2, July 3, and July 4, all on the under surface of new, young hackberry leaves, with the following exceptions: two egg bundles were seen on the upper surfaces of hackberry leaves, and a third egg-mass was found on the under side of a thumb-size hackberry branch.

No estimate could be made of the numbers of egg-masses laid on the leaves of large trees, but the egg-masses were removed daily, between July 3 and July 11, from one small (8-ft tall) hackberry tree, and 21 egg-masses were found during that period. At the rate of 350 eggs per mass, there were over 7000 eggs laid on this small tree.

Early in the day of July 2, 1951, there were noteworthy aggregations of Hackberry Butterflies on the wet mud surrounding little pools of rainwater along the road through the woods, but by that night most of the pools had dried up. A widespread distribution of butterflies took place during the night of July 2, so that on July 3, butterflies were visible everywhere on South Bass Island. No other endemic center developed, probably because the scattering was related to a search for moisture, and there may not have been mating and egg-laying in other locations.

During the night of July 2, butterflies gathered on mulberries on a tree near the tip of Oak Point, and on cherries on a tree on Peach Point, both sites about two miles from the endemic woodlot. They also gathered in great numbers at a cherry tree near the woodlot, and here Miss Louisa Fuchs demonstrated an observation she had made, that the butterflies scattered whenever she clapped her hands. This fact was corroborated several times, but the butterflies were not disturbed by an auto horn, nor by shouting and whistling.

At 10:00 AM, July 3, every cherry on the Fuchs tree was surrounded by clusters of 16 to 31 butterflies (fig. 6). Apparently, all of the butterflies had inserted their probosci through breaks in the cherry skin, and were sucking the cherries dry. We could not determine whether or not the butterflies were able to *make* the breaks in the cherry skin.

Butterfly eggs hatched between July 7 and 13, after an incubation period of 150 hr, at temperatures which were unrecorded. Dr. J. M. Speirs found the length of the newly-hatched larvae to be 1.8 mm. At the time of hatching, the larvae had whitish bodies capped with glossy black heads (fig. 7), but the larvae started eating hackberry leaves at once (fig. 8), and their bodies quickly became pale green.

The larvae ate actively for a short while, following a distinctive pattern. They were high in the trees, but not at the tree tops. They worked down-stem of each branch and left the terminal foliage of many branches undisturbed, and they ate downwards within the tree, thus leaving the tree tops foliated. The trees developed new lateral foliage on their branches, even if the defoliation had proceeded to the tip of the branches.

On July 19, 1951, twenty larvae ranged in length from 2.7 mm to 4.7 mm (avr. 3.6 mm). The numbers of larvae had undergone great reduction during the previous week, and most of the larvae still present were headed towards the mid-ribs of the leaves, away from the feeding areas (edges). These inactive larvae were held to the under surface of the leaves by silken patches, and we assume that a moult was occurring. There was no shortage of leaves available as food, so this change to inactivity was not associated with an "eat-out."

On July 24, 1951, there were many larvae on the leaves of the small tree which we had protected by removing eggs and larvae, and we think they had dropped there from an over-hanging branch. These larvae were inactive, and there were many silk patches on the leaves where larvae had been attached. We saw a spider carrying one of the larvae, and, since spiders had just spun new webs

throughout the woodlot, it is possible that spiders may have caused a notable decline in numbers of larvae.

Since egg-laying was spread over ten days, the larvae exhibited a corresponding range of size. Samples taken on July 29, 1951, ranged in length from 2.8 mm to 6.0 mm, and there were seven modes of frequencies, about 0.5 mm apart.

On August 5, 1951, there was noticeable change of color. The very rare individual which was seen eating was still green, while the others varied from pale green to very dark gray, so the color change was associated with cessation of eating.



FIGURE 6. Butterflies sucking juice out of cherries.

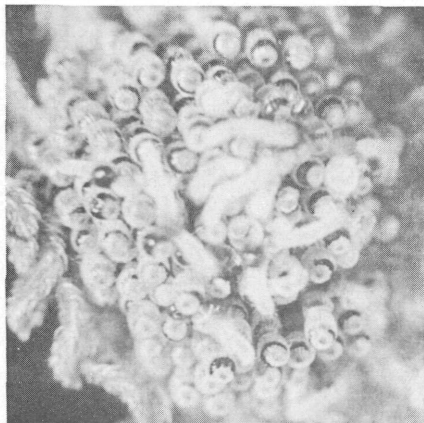


FIGURE 7. Larvae emerging from eggs of the Hackberry Butterfly.

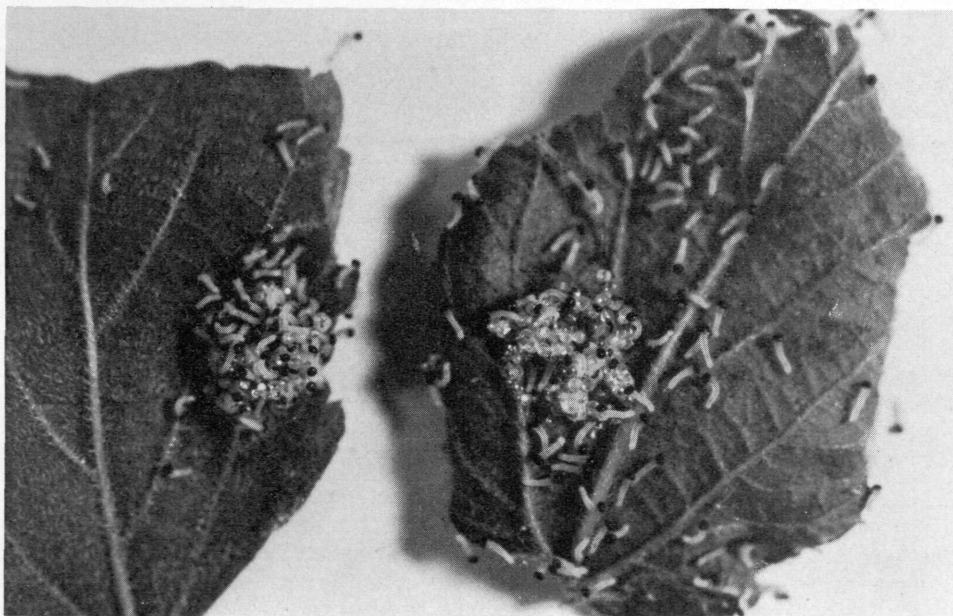


FIGURE 8. Larvae leaving egg-mass and starting to eat tissues of hackberry leaves.

By August 16, 1951, there were so few larvae left on the leaves that a sample of 63 inactive ones was collected with difficulty. These larvae ranged from 3.0 to 4.6 mm in length, and averaged 3.6 mm. By September 30, no larvae could be found on the trees, and no intensive search of the ground was made. Four inactive larvae were found on leaves on October 18, and the same ones were seen again on October 31, 1951.

No larvae could be found on May 4, 1952, but many larvae were found on May 10, eating the half-opened leaf buds and becoming green, while several hibernating larvae were found on twigs, near new leaves (avg. length 4.4 mm). On May 12 we found larvae with newly cast skins at the base of twig buds, and on May 16 there were many green larvae (avg. length 5.5 mm).

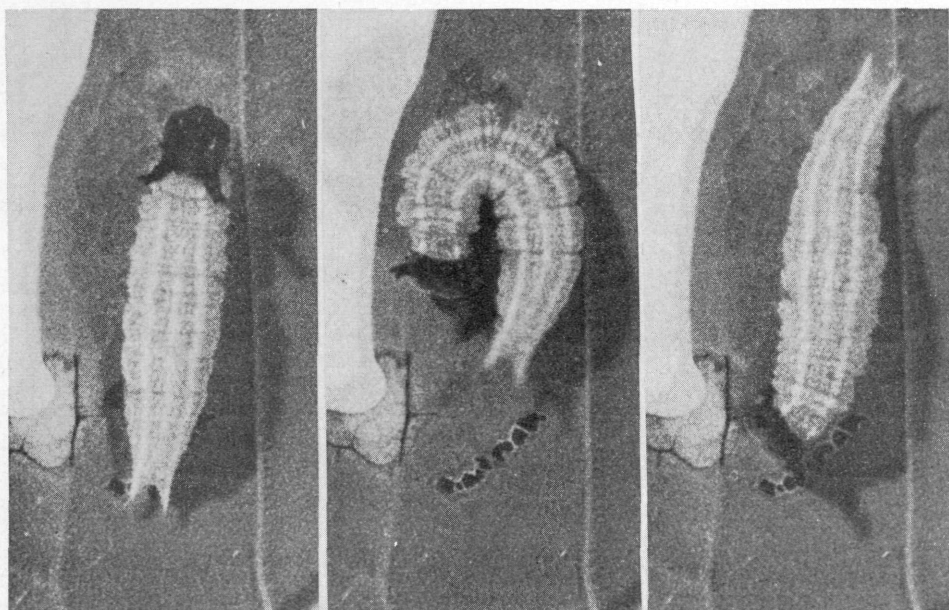


FIGURE 9a. Larva preparing to pupate by heading up-leaf and weaving a patch of silk.

FIGURE 9b. Larva reversing position to head down-leaf.

FIGURE 9c. Larva, tail attached to silk patch, hangs head down for pupation.

On May 20, 1952, a warm clear day after several chilly, rainy days, there was an up-trunk stream of larvae on the shady side of the tree. At 1:00 PM when found, there were none nearer the ground than $2\frac{1}{2}$ ft, and by 3:30 PM the wave had passed the 6-ft mark. On this date the gray larvae had an average length of 4.7 mm, while the green ones were 7.0 mm. Cool days followed, and on May 26 bright sunlight again raised air temperatures into the seventies. At 8:45 AM (temp. 61 F) the larvae on leaves were feeding, but none were showing up on the trunk. At 12:30 PM there were 23 active larvae between 5 and 6 ft up on the tree, and by 4:15 PM these larvae were scattered between 9 and 12 ft.

The larvae had defoliated most of the hackberry trees in the woodlot by June 11, 1952, when, in the heat of midday, they began a down-trunk migration. The migrants, ranging in length from 9 mm to 32 mm, promptly ascended herbs and trees, as noted before, for pupation. One was seen weaving its button of silk on a maple leaf on June 11 (fig. 9a, b, c), and the imago emerged from its pupa 8 days later (fig. 10).

It is a curious fact that the descent from hackberry trees and pupation on

other trees did not happen all at once in 1952 as it had on June 16, in 1951. Some larvae were still eating, and others were descending to pupate on through June 19. On June 17, measurements were made of larvae on basswood leaves, ready to pupate. The pupae ranged from 13 mm to 20 mm in length, and certain individuals were marked so as to establish relationships of size and sex of imago to size of pupating larvae.

1. 15 mm pupa, yielded a male with body length of 15 mm
2. 16 mm pupa, yielded a male with body length of 16 mm
3. 17.5 mm pupa, yielded a female with body length of 16 mm
4. 18.5 mm pupa, yielded a female with body length of 18 mm
5. 19.5 mm pupa, yielded a female with body length of 20 mm



FIGURE 10. Imago emerging from pupal case.

On June 19, 1952, the first butterflies of the season were seen, and the numbers increased daily to a peak about June 24. The absence of rainfall during this period left dry the holes in the road around which the hackberry butterflies had gathered in 1951, and this may help explain the fact that on June 26, 1952, the butterflies had scattered widely over South Bass Island. On June 28, the butterflies were actively dehydrating cherries and mulberries, as they did in 1951.

In spite of the 1952 drouth, a second set of leaves developed, though slowly, on the hackberry trees, and egg masses appeared on the new leaves. Hatching eggs were seen on July 2 and on succeeding days through July 10, but new-laid eggs were found as late as July 10. The overlap in stages in 1952 was much greater than in previous years, as shown by the fact that on July 10 there were present pupae, imagoes, new eggs, hatching eggs, new-born larvae, and big larvae.

By July 12, there were few butterflies present, and on July 17 there were no other stages present than young larvae. Many of these larvae had attained a length of 3 mm, and many of the second set of leaves had been stripped down to ribs and veins. The second eat-out was about complete on July 24, when, early in the morning, the woodlot was a tangled mess of silken strands, each strand

with a larva descending to the ground. These greenish larvae crawled on the ground to the nearest hackberry tree and started ascending it.

At 6:40 AM, on July 26, there were few larvae left on the branches, but some gray larvae were found on the trunks of the trees. At 2:00 PM, on July 27, there were great numbers of gray larvae moving restlessly, not up or down, on the tree trunks. At 9:00 AM, on July 29, larvae were tucking themselves into the crevices of the bark, many on some trees, few or none on others. One smooth-barked hackberry tree, *Celtis mississippiensis*, had clusters of larvae, each cluster several square inches in area, wherein each larvae seemed to be trying to hide behind each other larva. A stink-bug nymph on one such cluster was inserting its proboscis into the body of one larva after another (fig. 11).



FIGURE 11. Larvae clustered for hibernation, preyed upon by nymphal stink-bug.

Although no counts were made, we noted an annual increase in the number of pupae which were parasitized and killed by other insects. We saw small flies emerge from one pupa case, but neglected to collect them and get them identified. Scudder (1889: 1883 and 1921) stated that Riley (1882) had bred the dipterous parasite, *Phorocera edwardsii*, from *Chlorippe celtis*, and that Edwards, of West Virginia, had reared the hymenopterous parasite, *Limneria fugitiva* Say, from the same butterfly.

Records of the life-history of the Hackberry Butterfly in 1953, 1954, and 1955 are included in the following summarizing table (1), while growth records are shown in summary table 2.

TABLE 1
Life-history dates

Year	Green larvae	1st Defoliation	Pupation	Imagoes	Mating	Eggs	Hatching	2nd Defoliation	Greying Hibernation
1950		6-14	6-18			7-13	6-25, 28	8-20	
1951		6-10	6-16	6-23 to 7-14	6-28	7-1 to 7-11	7-7 to 7-13	not complete	7-24 to 8-5
1952,	5-10 to 5-20	6-11	6-11 to 7-10	6-19 to 7-12		7- to 7-10	7-2 to 7-10	7-24	7-24 to 7-26
1953,	5-9	6-17	6-17	6-22					7-19 to 8-2
1954,	5-6	6-14	6-14	6-22	6-27	6-29	7-4	7-24	7-24
1955,	5-10		none	few			7-6 (one batch)		

TABLE 2
Growth records

Eggs laid in clutches of 310 to 356 between July 1 and July 13.
Hatching after 150 hr, between July 7 and July 13.
Larvae: 1.8 mm at hatching.
3.6 mm on July 19. Range 2.7 to 4.7 mm
3.6 mm on August 20. Range 3.0 to 4.6 mm. 52 specimens
4.4 mm on May 10. 9 specimens
5.5 mm on May 16. 15 green specimens
7.0 mm on May 20. 19 green specimens
23.3 on June 11. 14 down-migrants, ranging from 9 mm to 32 mm
Pupae: 15 mm to 19.5 mm. Smaller ones yield males, larger ones yield females.
Imagoes: emerged from 8 day-old pupae.

DISCUSSION

The fact that the larvae of the Hackberry Butterfly had two eating seasons on South Bass Island, and accomplished phenomenal "eat-outs" in the hackberry woodlot seemed to be associated with different ways of approaching winter. In 1951, the newly-hatched larvae had not completely defoliated their host-trees when they quit eating, and turned grayish-brown. The silken attachments of the larvae on the under surface of hackberry leaves at that time was like those described by Riley. The lack of such areas in 1950 and in 1952 led to the alternative behavior of dropping from the leafless twigs to the ground, with immediate ascent up the trunks and hibernation in crevices of the bark, as found by Edwards, (quoted).

The fact that but one generation per year occurred on South Bass Island while two generations were found in Minnesota, two broods occurred in Virginia and West Virginia, and three broods southwards, may be associated with temperature, or with different degrees of summer drought, but it is attributable to the fact that only larvae over-wintered on the island while adults and larvae both hibernated at the sites of the other studies. There is also uncertainty as to the use of the words "brood" and "generation." A female who lays successive batches of eggs produces more than one brood. A generation encompasses the series of life-history stages from egg to egg.

A variation in the pattern of life-history accompanied the population explosion on South Bass Island, namely, an increase in the overlap of the several stages, year by year, and this may have made possible the biological control (parasitization) which terminated the explosion abruptly. While the larvae of 1950 all quit eating, descended from the hackberry trees, ascended other trees, pupated at the

same time, and the adults were terrifically abundant at the mating time and place, those of each succeeding year-group diverged ever wider from this coincidence. On a single day in 1954, large larvae, pupae, imagoes, eggs, and newly-hatched larvae were all collected. This increased spread could explain the records of late adults elsewhere and the interpretation of two broods per year. There is no indication that any of the butterflies on South Bass Island laid more than a single set of eggs.

The death of large numbers of hackberry trees in the woodlot by 1954, due surely to the inability of defoliated trees to photosynthesize, had so reduced the hosts of the butterflies in this endemic center that hibernating larvae were very scarce in December, 1954. There seemed to be more scattering of butterflies from this woodlot to other hackberry trees on the island in 1954 than had been noted before, and this may have been associated with the need for moisture.



FIGURE 12. Edge of woodlot, showing trees killed by larvae of the Hackberry Butterfly.

Small black engraver beetles, probably *Scolytus muticus* Say, according to Prof. Josef Knull, bored round holes through the bark of dying trees, and the exudate at these holes supplied the moisture needed by many butterflies, so each such exuding hole was surrounded by clusters of butterflies. The beetle larvae thrived, and the tree bark became so loose that it sloughed off. The woodlot, with its bare dead trunks, resembled an area hit by fire or by flood (fig. 12).

Concern over this unpleasant landscape led some people to ask for action to control the devastating butterfly larvae. No action was taken, fortunately, because the normal succession from hackberry trees to maple, ash, and oak trees is proceeding more rapidly than it could have without the help of the butterflies. henbit, and bedstraw was lush, while in other woods the ground was sere and bare. and sunshine reached the floor of the woodlot. By September 23, 1950, the ground cover of seedling Robert's geranium, sweet cicely, motherwort, chickweed, henbit, and bedstraw was lush, while in other woods the ground was sere and bare.

On October 31, 1950, this lush herbage was being eaten by land snails and rabbits. The area had become a pleasant woodlot, without hackberry trees, in 1962.

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